

A revision of *Weinmannia* (Cunoniaceae) in Malesia and the Pacific. 4. The Society, Marquesas and Austral Islands

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ABSTRACT

Six species are recognized in this region, all belonging to sect. *Leiospermum*. *Weinmannia rapensis* is confined to Rapa in the Austral Islands and its reported occurrence in Pitcairn is discussed. *Weinmannia parviflora* occurs on most of the large islands of the Societies except Raiatea and its leaf shape and indumentum vary with its ecology. *Weinmannia vescoi* and *W. raiateensis* are both confined to Raiatea. In the Marquesas, *W. marquesana* is represented by two varieties and a distinctive, new species, *W. tremuloides*, is described and illustrated from Fatu Hiva.

RÉSUMÉ

Six espèces, appartenant à la sect. *Leiospermum*, sont reconnues pour la région. *Weinmannia rapensis* est confiné à l'île de Rapa dans les Australes et sa présence à Pitcairn est discutée. *Weinmannia parviflora* se rencontre dans la plupart des grandes îles de la Société, sauf à Raiatea, avec une grande variabilité dans la forme des feuilles et la pubescence. *Weinmannia vescoi* et *W. raiateensis* sont tous deux propres à Raiatea. Pour les Marquises, *W. marquesana* compte deux variétés et une espèce nouvelle, *W. tremuloides*, endémique de Fatu Hiva, décrite ici et illustrée.

MOTS CLÉS
Weinmannia,
Cunoniaceae,
Îles de la Société,
Îles Marquises,
Rapa.

In SE Polynesia, to the east of the Cook Islands, *Weinmannia* is found in the Society Islands, the Marquesas Islands, and on Rapa in the Austral Islands. The genus is a significant component of the vegetation on Tahiti and on several of the Marquesas, in contrast to much of the Malesian-Pacific region where it is generally locally common at most.

With the exception of *Weinmannia rapensis* which is morphologically distinct and geographically isolated, material from this region of the Pacific is rather variable, especially in the shape, size and texture of the leaves. This treatment recognises five species from the Society and Marquesas Islands, including a new one from Fatu Hiva (Table 1).

The leaves of the newly named species are very distinctive but the remaining taxa are inclined to grade into one another to some extent, and the characters that differentiate between them often overlap or are not completely diagnostic. Provenance must therefore be used occasionally in identification. While this is not generally a recommended taxonomic practice, the under-

lying morphological and geographical patterns would otherwise be lost.

For example, *Weinmannia parviflora* appears to be confined to the Society Islands but a few specimens from the Marquesas (belonging *W. marquesana* var. *marquesana*) are vegetatively difficult to distinguish from it. Most collections of *W. raiateensis* have small, delicate leaves but a few have larger ones and/or some unifoliolate leaves, and thus resemble some specimens of *W. parviflora* from Tahiti. Material from Huahine, designated here as *W. parviflora*, is somewhat intermediate between that species and *W. raiateensis* (in having caducous stipules and winged petioles when the leaves are trifoliolate).

A large number of recent collections, especially by J. FLORENCE, provide a detailed picture of variation in relation to ecology and distribution. *Weinmannia parviflora* and *W. marquesana* especially show phenotypic variation correlated with altitude and exposure. At mid elevation on Tahiti, *W. parviflora* has narrowly elliptical leaves with a crenate-sinuate margin, while at higher altitude the leaves are shorter and often ovate, the stems

TABLE 1.—The species of *Weinmannia* in the SE Polynesia according to recent treatments.

Current revision	Bernardi (1964)	Fosberg & Sachet (1972)	Florence (1982)
Society Islands			
<i>W. parviflora</i>	<i>W. parviflora</i>	<i>W. parviflora</i> var. <i>parviflora</i> (by implication)	<i>W. parviflora</i> var. <i>parviflora</i>
<i>W. vescoi</i> (syn. <i>W. ovalifolia</i>)	<i>W. vescoi</i> (syn. <i>W. ovalifolia</i>)		<i>W. vescoi</i>
<i>W. raiateensis</i>	in synonymy under <i>W. vitiensis</i>		<i>W. raiateensis</i>
Marquesas Islands			
<i>W. marquesana</i> var. <i>marquesana</i>	<i>W. marquesana</i>	<i>W. parviflora</i> var. <i>marquesana</i> + <i>W. parviflora</i> var. <i>glabrata</i>	
<i>W. marquesana</i> var. <i>myrsinites</i>		<i>W. parviflora</i> var. <i>myrsinites</i>	
<i>W. tremuloides</i>			
Austral Islands			
<i>W. rapensis</i>	<i>W. rapensis</i>		<i>W. rapensis</i>

are thicker and often more densely pubescent, the internodes are shorter and the leaf margin is almost entire. A similar pattern is seen, though rarely, in *W. marquesana*. It appears that these high altitude forms have evolved in parallel on Tahiti and in the Marquesas. *Weinmannia parviflora* is absent from Raiatea and material with rounded leaves and short, glabrous internodes (*W. vescoi*) is not obviously derived from any other taxon. Thus on Raiatea, Tahiti and some of the Marquesas, there are specimens from relatively exposed, windswept sites at high altitude with ovate or rounded, coriaceous leaves and short internodes, but they all belong to different taxa depending on the island on which they occur.

Weinmannia has small, comose, anaemochorous seeds that appear to be well adapted to wind dispersal. It is thus not surprising that representatives of the genus are found on all the high volcanic islands of this region. The seeds of *W.*

marquesana, *W. raiateensis* and *W. vescoi* are similar to one another and unusual in sect. *Leiospermum* in that the comose hairs are relatively short, and shorter than those of *W. parviflora* from Tahiti. If the presence of these hairs is related to dispersal, this could indicate a decline in the dispersability of these three taxa. The Iles sous le Vent (including Raiatea, Tahaa, Huahine, Bora Bora) and the Marquesas are older than the Iles du Vent (Tahiti and Moorea), Tahiti being about one million years old (see BROUSSE 1993).

A generic description applicable to the Pacific species of *Weinmannia*, and general notes on morphology, are given in HOPKINS (1998a). All the species of the region dealt with here belong to sect. *Leiospermum*, whose characters are also discussed in HOPKINS (1998a). An index to all the taxa of Malesian-Pacific *Weinmannia* (see HOPKINS 1998a,b,c) is given at the end of this paper.

Key to the species and varieties of *Weinmannia* in the C Pacific

1. Leaves usually trifoliolate 2
- 1'. Leaves usually simple (unifoliolate) 4
2. Young stems \pm glabrous, petiole usually glabrous; stipules not recurved and usually caducous 3
- 2'. Young stems densely pubescent, petiole semiterete but not winged, pubescent; stipules strongly recurved and usually persistent (Rapa) **6. *W. rapensis***
3. Petiole laterally flattened and U-shaped in cross section (Fatu Hiva) **5. *W. tremuloides***
- 3'. Petiole \pm flat on adaxial surface, not laterally flattened (Raiatea) **2. *W. raiateensis***
(and rarely some specimens of *W. parviflora* but not on Raiatea)
4. Young stems completely glabrous (Raiatea) **3. *W. vescoi***
- 4'. Young stems with sparse to dense indumentum 5
5. Stipules usually persistent and elliptical, recurved, the apex rounded; capsules small, 2.5-3.5 mm long at dehiscence (Society Islands) **1. *W. parviflora***
- 5'. Stipules usually caducous, when present usually \pm round, conduplicate, the apex acute and the margin sometimes toothed, or sometimes stipules elliptical-ligulate; capsules larger, 3.3-5 mm at dehiscence (Marquesas) 6
6. Leaves elliptical or ovate, large (2.5-)3.3-7.5 \times (1-)1.3-3.6(-4.4) cm, venation usually visible on adaxial surface and reticulum on abaxial surface not dense **4a. *W. marquesana* var. *marquesana***
- 6'. Leaves ovate, smaller, 1.6-2.7(-3.3) \times 0.7-1.7 cm, venation obscure on adaxial surface and reticulum on abaxial surface dense **4b. *W. marquesana* var. *myrsinites***

1. *Weinmannia parviflora* G. Forst.

Fl. Ins. Austr.: 29 (1786); Willd., Sp. Pl., ed. 4, 2: 438 (1799); Poir., Encycl. 7: 580 (1806); A. Gray, U.S. Expl. Exped., Phan. 1: 673, Atlas t. 85A, Fig. 1-5 (1856) p.p.; Decne., Voy. Vénus, Bot. Texte: 26, Atlas t. 20 (1846); Seem., Fl. Vit.: 109 (1865); Engl., Linnaea 36: 647 (1870) pro parte, Nat. Pflanzenfam.,

ed. 2, 18a: 256 (1930); Bernardi, Bot. Jahrb. Syst. 83: 195, t. 39 (1964); Fosberg & Sachet, Micronesica 8: 44 (1972).—*Leiospermum parviflorum* (G. Forst.) D. Don, Edinburgh New Philos. J. 9: 91 (1830) pro parte excl. spec. New Zealand.—*Merrettia terminalis* Banks & Sol., mss. *Marattia terminalis* Sol. in Parkinson, Drawings of Tahit. Pl., t. 48, ex Seem., Fl. Vit.: 109 (1865), pro syn. sub *Weinmannia parviflora*; Britten, J. Bot. 45: 315 (1907).—*Weinmannia parvi-*

flora var. *parviflora*; implied by Fosberg & Sachet, *Micronesica* 8: 44 (1972).—Type: *Forster s.n.*, s.loc., Pallas Hb. (lecto- here designated, BM! pro parte excl. left hand part of sheet).

Shrub or tree 1-10(-12) m high and up to 45 cm dbh. Branching usually not dichotomous at lower elevation, more often dichotomous at high elevation. Young stems usually densely covered in erect, stiff hairs ca. 0.4 mm long, sometimes glabrate; at lower altitudes, internodes up to 5 cm long; at high altitude internodes usually short, 0.5-1.5 mm long, the stems often thick, up to 0.3 mm diameter and nodes thickened, older stems glabrescent, ca. 0.5 mm diameter with numerous pale lenticels. Stipules usually persistent at several nodes on reproductive shoots (except Moorea and Huahine), elliptical, spatulate or \pm orbicular, the margins recurved and the whole stipule recurved, $0.4-0.5(-0.9) \times 0.5-0.6(-0.8)$ cm, the apex rounded, puberulent on both surfaces, venation usually indented above. Leaves usually unifoliate, sometimes mixed with trifoliate ones. Unifoliate leaves somewhat variable in shape and texture according to altitude: at mid altitude, subsessile to petiolate, the petiole \pm terete to semiterete, 0.2-1 cm long, the blade usually narrowly elliptical, $3.5-8.8 \times 1.2-3(-3.5)$ cm, the base either acute and decurrent into the petiole or more truncate with a sharp distinction between petiole and blade, apex acute, the blade chartaceous, sometimes punctate below, the margin sometimes thickened, crenate, dentate or sinuate and sometimes undulate, 10-15 notches on each side of a leaf; at higher altitude, shortly petiolate, the petiole ca. 0.3 mm or 0.5 mm if blade cuneate at base, the blade $3.1-5.7(-7) \times (1.5-1.9) \times 3.3(-4.2)$ cm, ovate to oblong, the base usually truncate, the apex broadly acute to obtuse (rarely rounded), coriaceous or subcoriaceous, margin crenulate. Trifoliate leaves up to 9 cm in length, the petiole 1-1.5 cm long; on Tahiti the petiole terete to semiterete, the upper surface not winged; on Moorea and Huahine, the petiole narrowly winged; lateral leaflets acute and unequal at base; terminal leaflet long-attenuate at base.

Inflorescence a pentad (especially at high elevation) or heptad, often with additional racemes arising at the lower most node of the inflorescen-

ce from lateral auxiliary buds; reduced leaves sometimes present at nodes within inflorescence; peduncles and rachis segments 0.5-4 cm long, shorter at higher altitude, puberulent; racemes up to 13.5 cm long at lower altitude and to 6 (-9.5) cm long at high altitude. Stipules at nodes within inflorescence smaller than at vegetative nodes. Floral buds inserted singly; floral bracts to 0.4-0.7 mm long, subcarinate, strigose-puberulent, usually caducous. Flowers usually unisexual, rarely bisexual or ?protandrous; pedicel 0.8-2.5 mm long, puberulent; calyx lobes 0.4-0.9 mm long, puberulent on outer surface; corolla oblong to \pm bluntly triangular, $0.7-1.6 \times 0.5-1.5$ mm; disc lobes 0.3-0.7 mm long; in male flowers: filaments 1.9-3 mm long, the ovary 0.5-0.9 mm long, puberulent and the style 0.1-0.2 mm long, curved inwards; in female flowers: filaments 0.7-1.1 mm long, the ovary > 1.1 mm long at anthesis, puberulent, and the styles > 0.7 mm long, \pm straight, the stigmas capitate and papillose.

Capsules $2.5-3.5 \times 1.5$ mm at dehiscence (up to 0.5 mm longer prior to dehiscence), the styles 0.5-0.8(-1) mm long; the exocarp sparsely puberulent to almost glabrous, endocarp sometimes separating from exocarp in old fruits; calyx lobes usually caducous; central column present. Seeds 0.8-1 mm long, comose at each end, the hairs 0.5-0.7 mm long.—Fig. 1A-K, 2.

JUVENILE FOLIAGE (high altitude).—The seedling attached to *van Balgooy 1796* has simple, chartaceous leaves, up to 6.5×5.5 cm, with the margin dentate, the stipules much as in the adult foliage and the stem ca. 3 mm thick, woody but only sparsely hairy.

BREEDING SYSTEM.—Polygamodioecious. While the flowers on most specimens are either male or female, a few collections have racemes of mostly male flowers with a few bisexual ones mixed in (e.g. *Hoogland & Florence 12920*), and others have male flowers and fruit on the same specimen (*Gagné & Montgomery 2362*).

FIELD CHARACTERS.—At lower elevations, frequently a small tree and at high elevation, a shrub or gnarled tree, the branches sometimes clothed in bryophytes. Wood red, hard (*Florence & Varney 11093*) or blaze pink and wood creamy

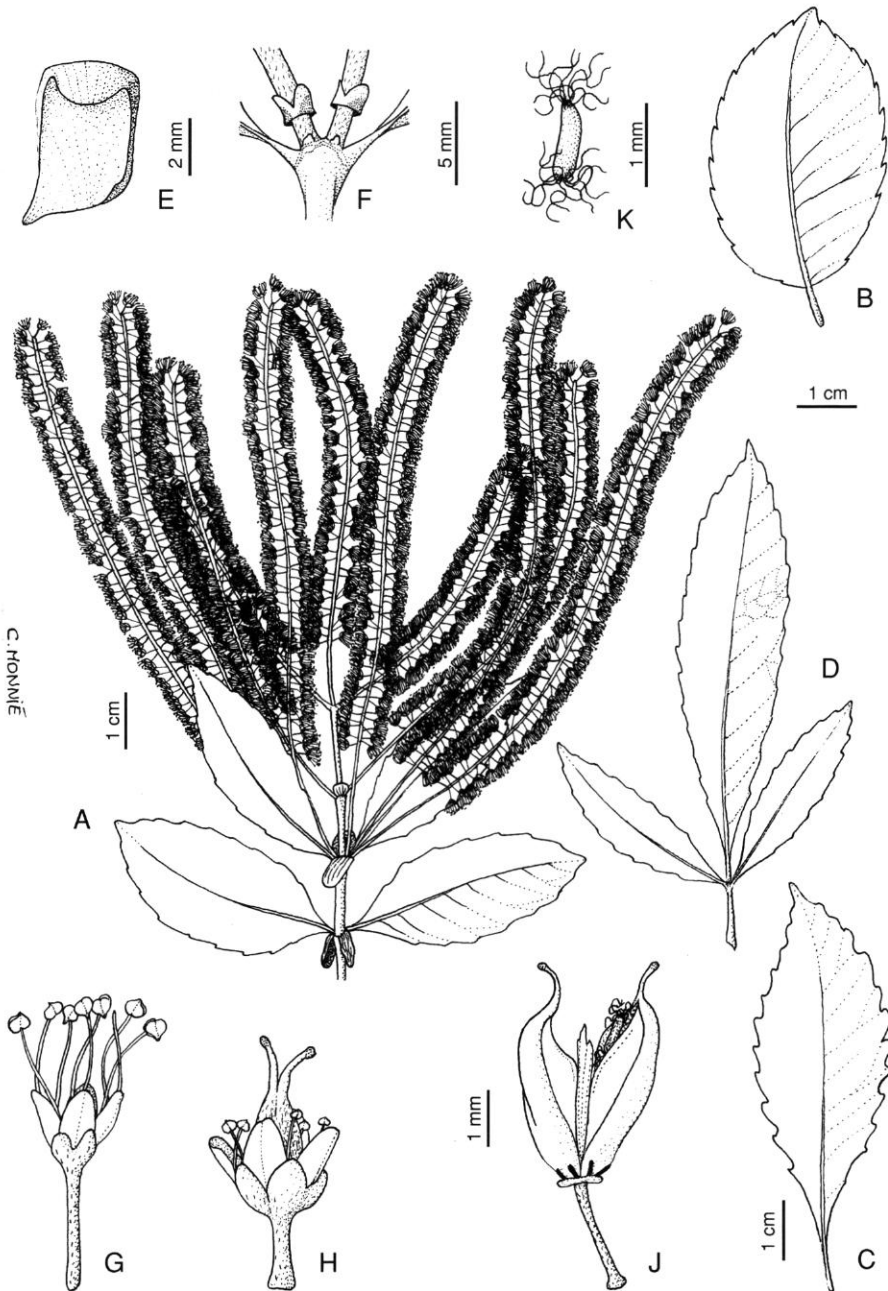


Fig. 1.—A-K, *Weinmannia parviflora*: A, flowering shoot, the leaves typical for mid altitude on Tahiti and the inflorescence a heptad with additional racemes at the lowest node, developing from lateral auxiliary buds; B, leaf, typical of plants from exposed locations at high altitude on Tahiti; C, leaf, from Moorea; D, trifoliate leaf, Tahiti; E, stipule with recurved margins; F, detail of node with 2 opposite petioles and the peduncles of 2 partial inflorescences, the apical bud aborted; each peduncle with a "collar" (remnants of fused stipules that protect the inflorescence in bud) and lateral auxiliary buds at base; G, male flower; H, female flower; J, dehiscent capsule with persistent central column and one seed remaining in locule; K, seed. (A, E, G, Florence 9090; B, St. John & Fosberg 17146; C, Florence 8365; D, H-K, Florence 9089; F, Florence 3110).—Drawn by C. MONNIÉ.

(*van Balgooy 1685*). Leaves pale green or bright green above, shiny, coriaceous. Inflorescence axes and calyx show a colour polymorphism at lower altitudes, being either pale green or purple-red, but above 1500 m only the red form was observed (J.C. BRADFORD pers. comm.). Buds white or red. Flowers with pedicel and sepals pinkish, pale purple or green, petals and stamens white, disc segments pale purple or dark, anthers yellow, ovary white or pale green, the stigmas pinkish in female flowers (specimen field labels and J.C. BRADFORD pers. comm.). Reported as odourless (*Quayle 39*) or sweetly scented and visited by bees (J.C. BRADFORD pers. comm.). Fruit green sometimes tinged with red, reddish, or pale purple; later brown.

DISTRIBUTION AND ECOLOGY.—Abundant on Tahiti and also occurring on Moorea, Huahine and Bora Bora [*vide FLORENCE (1982)*, who reports that *Dumont d'Urville 200* (s.l., s.d.) is from that island]. Also grows on Tahaa (J. FLORENCE pers. obs.).

On Huahine, confined to the central crest between Mt. Matoereere and Mt. Turi, from 450 m to the summit (670 m), in forest dominated by *Metrosideros* and *Macaranga*, growing with *Alstonia* and *Myrsine*, and especially recorded from ridges. On Moorea, first appearing around 400-500 m, and co-dominant with *Metrosideros* in mesic forest and more abundant in cloud forest with *Ilex*, *Myrsine* and *Metrosideros* up to 1200 m. On Tahiti, probably the most abundant woody plant in undisturbed forest from 400 m to the summit of the island, Mt. Orohena, at 2241 m. Co-dominant with *Metrosideros* as the main structural element of slope and ridge forest at medium and high elevations and practically ubiquitous. Other associates in moss-covered shrubbery at high altitude in the typical *Weinmannia-Alstonia* forest (FLORENCE 1993) include *Myrsine*, *Coprosma*, *Cyathea*, *Alstonia*, *Vaccinium*, *Alyxia*, *Reynoldsia*, and *Ilex*. At lower elevations, it occurs with *Alphitonia*, *Dodonea* and *Psidium* and is also found in scrub, on *Dicranopteris*-covered slopes and on steep wooded escarpments.

SELECTED COLLECTIONS (from a total of 88 studied).—**SOCIETY ISLANDS:** *Bora Bora?*: *Dumont*

d'Urville 200, s.loc., fr. (P). **Huahine:** *Florence & Tabuaitu 11627*, crête entre les Mts. Mato Ereere et Moua Turi, 16°43'S-151°01'W, 610 m, fl., 30 Oct. 1992 (P, PAP); *Grant 5314*, Distr. Maeva, Matoereere, 1710 ft., fl., 7 Feb. 1931 (BISH); *Grant 5316*, seedling (BISH); *St. John 17159*, Huahine Nui, Mt. Matoereere, N ridge, 650 m, fr., 1 Oct. 1934 (A, BISH, K, P). **Moorea:** *Florence 7935*, Haumi, crête SE du Mt. Tohica, 17°33'S-149°49'W, 860 m, fl., 22 Oct. 1986 (BISH, K, P, PAP); *Florence 8365*, Mt. Tohica, sommet N, 17°33'S-149°49'W, 1200 m, buds, 9 July 1987 (BISH, P, PAP); *Smith 174*, plateau above Afareaitu, fl., 8 June 1967 (A, BISH). **Tahiti:** *Adamson 40*, Distr. of Hitiaa, 400 m, buds, 19 Nov. 1928 (BISH); *Carlquist 655*, between Rocher du Diable and Fare Mato on Aorai Mt., 4200 ft., fr., 15 June 1962 (GH); *Florence 2291*, sentier captage d'eau du Belvédère, 17°34'S-149°31'W, 620 m, fr., 14 Jan. 1982 (P, PAP); *Florence 2315*, sentier du Mt. Marau, au Pic Vert, 17°37'S-149°32'W, 1405 m, fl., fr., 28 Jan. 1982 (BISH, P, PAP); *Florence 3277*, Mt. Marau, env. du relais TV, 17°37'S-149°32'W, 1430 m, yfr., 5 June 1982 (BISH, K, P, PAP); *Florence 3353*, route du Pic Rouge, Propriété Lévy, 17°35'S-149°33'W, 630 m, fr., 17 June 1982 (BISH, K, P, PAP); *Florence 3645*, crête W de la Papenoo, sentier de l'Orohena, 17°33'S-149°26'W, 915 m, fr., 3 Aug. 1982 (BISH, K, P, PAP); *Florence 5462*, Mahina, sommet du Mt. Pitohiti, sentier de l'Orohena, 17°37'S-149°28'W, 2110 m, fr., 19 Oct. 1983 (P, PAP); *Florence 7186*, Mahina, sommet N de l'Orohena, flanc S, 17°37'S-149°29'W, 2215 m, buds, 16 Nov. 1984 (P, PAP); *Florence 9088*, Faaa, route du Mt. Marau, km 6.5, 17°37'S-149°34'W, 1080 m, fl., 11 Feb. 1988 (BISH, P, PAP); *Florence & Varney 11093*, Punaauia, vallée Maruapo, crête N, 17°39'S-149°35'W, 880 m, fl., 13 Feb. 1992 (P, PAP); *Fosberg 62927*, NW slope up to Pic Vert, headwaters of side branches of R. Tipaerui, 640-650 m, fr., 17 June 1982 (BISH, BM, K, P, PAP); *Gagné & Montgomery 2362*, Mt. Orohena, 2240 m, fl., 11 Sep. 1988 (BISH); *Gagné 1013*, Mt. Marau, 1493 m, buds, fr., 30 June 1977 (BISH, P); *Grant 3601*, Dist. Punaauia, Diadem, 3275 ft., fl., 14 May 1930 (BISH); *Hoogland & Florence 12916*, Faaa, Mt. Marau, ridge towards Pic Vert, below TV station, 1380 m, fl., 14 Mar. 1994 (MO, P, PAP); *Hoogland & Florence 12918*, ridge between Upper Faatautia River and Paaraura valley, 600 m, fr., 16 Mar. 1994 (MO, P, PAP); *Hoogland & Florence 12927*, Tairapu Peninsula, plateau de Taravao along ridge track in upper Amoa catchment, 680 m, fr., 17 Mar. 1994 (MO, P, PAP); *Hoogland & Florence 12931*, between Lac Vaihiria and Cōl Urufaau, 650 m, fl., 24 Mar. 1994 (MO, P, PAP); *MacDaniels 1313*, S side Orohena, 1500 m, fl., 16 May 1927 (A, BISH, K); *MacKee 3056*, plateau below summit of Mt. Aorai, 1800-2000 m, fl., 27 Aug. 1955 (K); *Moseley, Challenger Expedition s.n.*, s.loc., 4000 ft., Sep. 1875,

(BM, K); *Nadeaud 413*, crêtes du Pinai et du Taffi, fl., Dec. 1856 (P); *Quayle 39*, Mt. Aorai Trail, leeward, 1694 m, fl., fr., 22 Sep. 1921 (BISH, K); *Raynal & Taureau 16539*, piste de l'Aorai, entre Belvédère et Fare Hamuta, 600 m, buds, 6 Oct. 1971 (P); *St. John & Fosberg 17146*, Orofena, S ridge, 1570 m, fr., 25 Sep. 1934 (A, BISH, P); *Teraoka & Kennedy 113*, Papenoo, back of Eric Garnier property, fr., 6 Sep. 1979 (BISH); *van Balgooy 1790*, NW ridge of Aorai, 1700 m, fl., fr., 22 Sep. 1971 (L).

LOCAL NAMES.—Aito; Aito mou'a; Ouru. Local uses: firewood (*Quayle 39*).

TIPIFICATION.—*Weinmannia parviflora* was the first species in the genus to be described from this part of the Pacific and its taxonomic history is discussed by BERNARDI (1964: 195). It was described by G. FORSTER, who with his father, was naturalist on the second of Captain COOK'S circumnavigational voyages in the H.M.S. Resolution from 1772 to 1775 (FOSBERG 1993). According to MERRILL (1954: 206), the name *W. parviflora* was one of several that were appropriated by FORSTER from the unpublished manuscript of SOLANDER and for which the latter had already prepared a detailed description based on the BANKS & SOLANDER collections from the first of COOK'S voyages. However, many of the descriptions in FORSTER'S Prodrum (1786) were actually written during the second voyage and D. NICOLSON (pers. comm.), who is studying the FORSTER types, considers it entirely appropriate to choose one of the specimens in the FORSTER collections as the lectotype.

The sheet selected at BM contains two elements. The right hand piece is designated as the lectotype of *Weinmannia parviflora* and the left hand piece belongs to *W. racemosa* L. f. from New Zealand. Both of COOK'S expeditions went on to collect in New Zealand after visiting Tahiti. Records of *W. parviflora*, mostly under the name *Leiospermum parviflorum*, from New Zealand [e.g. by D. DON (1830), WALPERS (1846), G. DON (1834)] are due to confusion with *W. racemosa*. Both species usually have simple leaves of similar size but the inflorescence structure is different (see HOPKINS 1998a).

Several early authors [e.g. GRAY (1854), MUELLER (1858), SEEMANN (1865), DRAKE

(1890)] also included material of *Weinmannia rapensis* in their concept of *W. parviflora*, based on *Cuming 1428*. These records from Elizabeth Island, (now Henderson Island in the Pitcairn group) are discussed under *W. rapensis*.

VARIATION.—*Weinmannia parviflora* is especially variable in the shape of its leaves or leaflets, but the young stems are usually pubescent and the stipules strongly recurved and usually persistent. On Tahiti, *W. parviflora* shows variation in leaf shape with altitude, and our concept of this species differs from BERNARDI'S in including all the high altitude material with ovate or rounded leaves here, rather than in *W. vescoi*, which is endemic to Raiatea. At middle elevations, the internodes of *W. parviflora* are relatively long and the leaves are usually narrowly elliptical with the margins markedly crenate or sinuate (Fig. 1A), and some trifoliolate leaves occur (Fig. 1D). At high elevation, in the central massif on Mt. Aorai, Mt. Orohena and Pito Hiti, the leaves are often shorter, usually oblong or ovate and the margins less markedly crenate (Fig. 1B) and the internodes are short, so that the overall habit resembles that of *W. vescoi*. Between 1500-1600 m on the flanks of Mt. Aorai, adjacent trees can have contrasting leaf morphologies (J.C. BRADFORD pers. comm.). Most collections are densely pubescent on the young stems but a few are glabrous (e.g. *Gagné & Montgomery 2362*, *Florence 7186*; *Florence 5464* is ± glabrous).

Material from Huahine, designated here as *Weinmannia parviflora*, has some similarities with *W. raiaateensis* since the stipules are caducous and the petioles are winged when the leaves are trifoliolate. Collections from Moorea also differ somewhat from *W. parviflora* in Tahiti as the stems are more or less glabrous, the stipules are rarely persistent and the leaves, although unifoliolate, have a rather sinuate and/or undulate margin (Fig. 1C).

2. *Weinmannia raiaateensis* J.W. Moore

Bernice P. Bishop. Mus. Bull. 102: 29 (1933); Bernardi, Bot. Jahrb. Syst. 83: 207 (1964) under *W. vitiensis*.—Type: *J.W. Moore 396*, Society Islands,

Raiatea, on high ridge between Vairahi and Avera Rahi valleys, 300 m, 3 Dec. 1926 (holo-, BISH; iso-, BISH!, P! 2 sheets).

Shrub or small tree 0.4-5 m high. Branching sometimes dichotomous. Nodes scarcely thickened and annular scar not prominent; internodes 0.5-3.8 cm. Young stems sparsely strigose-pubescent or glabrous. Stipules caducous or not, elliptical, shortly spatulate to ligulate, sometimes recurved, 0.7-1.1 × 0.4-0.6 cm, apex rounded to obtuse, ± glabrous with short, adpressed hairs towards base on abaxial surface. Leaves mostly trifoliolate, sometimes some unifoliolate, total length up to 9.7 cm (for a trifoliolate leaf) including a petiole of 0.4-2.4 cm; petiole semiterete and narrowly winged especially towards point of insertion of leaflets, glabrous or rarely pubescent above or below; leaflets narrowly elliptical, elliptical or narrowly obovate, the lateral ones 2.3-6 × 0.7-1.7 cm, base cuneate and unequal, apex acute, the terminal ones 3.8-8.3 (including a petiolule of 0.4-1.5) × 1.2-1.9 cm,

base long attenuate, apex usually acute, often broken; the blade glabrous on both sides, chartaceous to subcoriaceous, not punctate; margin sometimes thick-ened, crenate, 9-14 notches on each side of a leaflet, midrib flat or slightly raised above, prominent below, secondary and tertiary venation flat or slightly raised on both sides.

Inflorescence rather variable and nodes often asymmetrically branched; either a central triad or pentad, or two lateral triads, the apical bud aborted; often arising at nodes other than the most distal on a shoot; peduncle and rachis segments shortly and sometimes densely pubescent, peduncle 0.6-1.1 cm long, rachis segments up to 5 cm long. Floral buds inserted singly; floral bracts 0.6-0.7 mm long, scarcely longer than the buds, ligulate, ± glabrous, caducous. Flowers unisexual (male, *Gagné 1457*; female, *Florence 8945*); pedicel 1-1.7 mm long; calyx lobes 0.6-0.7 mm long, glabrous; petals 1.1-1.3 × 0.8 mm, oblong; in male flower: filaments ca. 2.5 mm long, disc lobes 0.4 mm long, ovary 0.7 mm long, pubescent, styles 0.1 mm long, incurled; in female

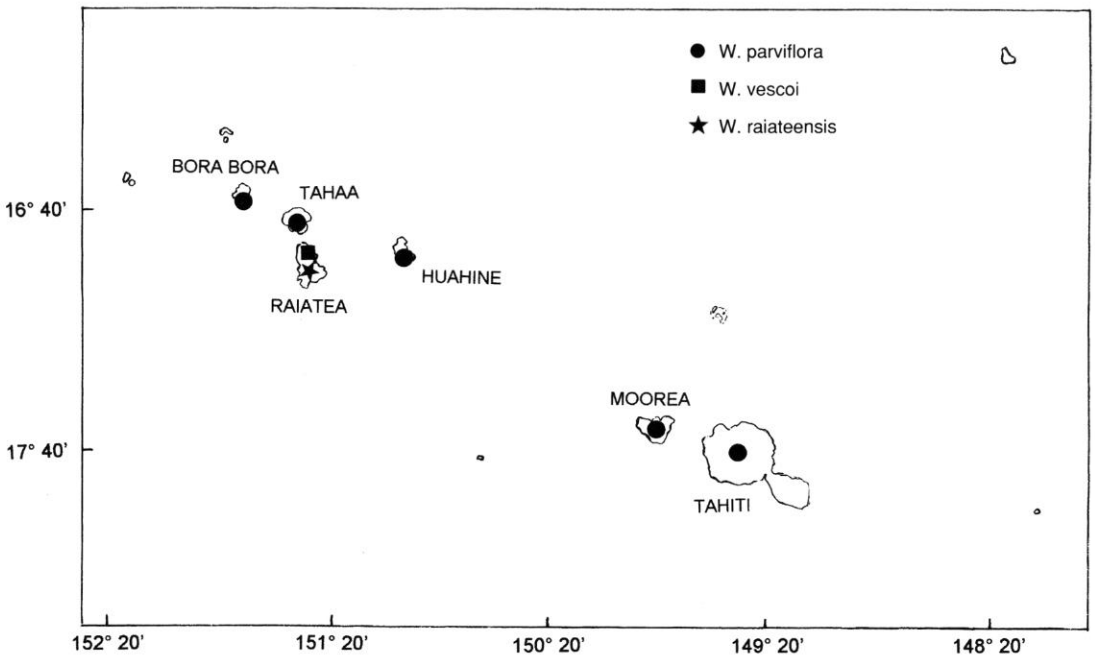


Fig. 2.—Distribution of *Weinmannia* in the Society Islands.

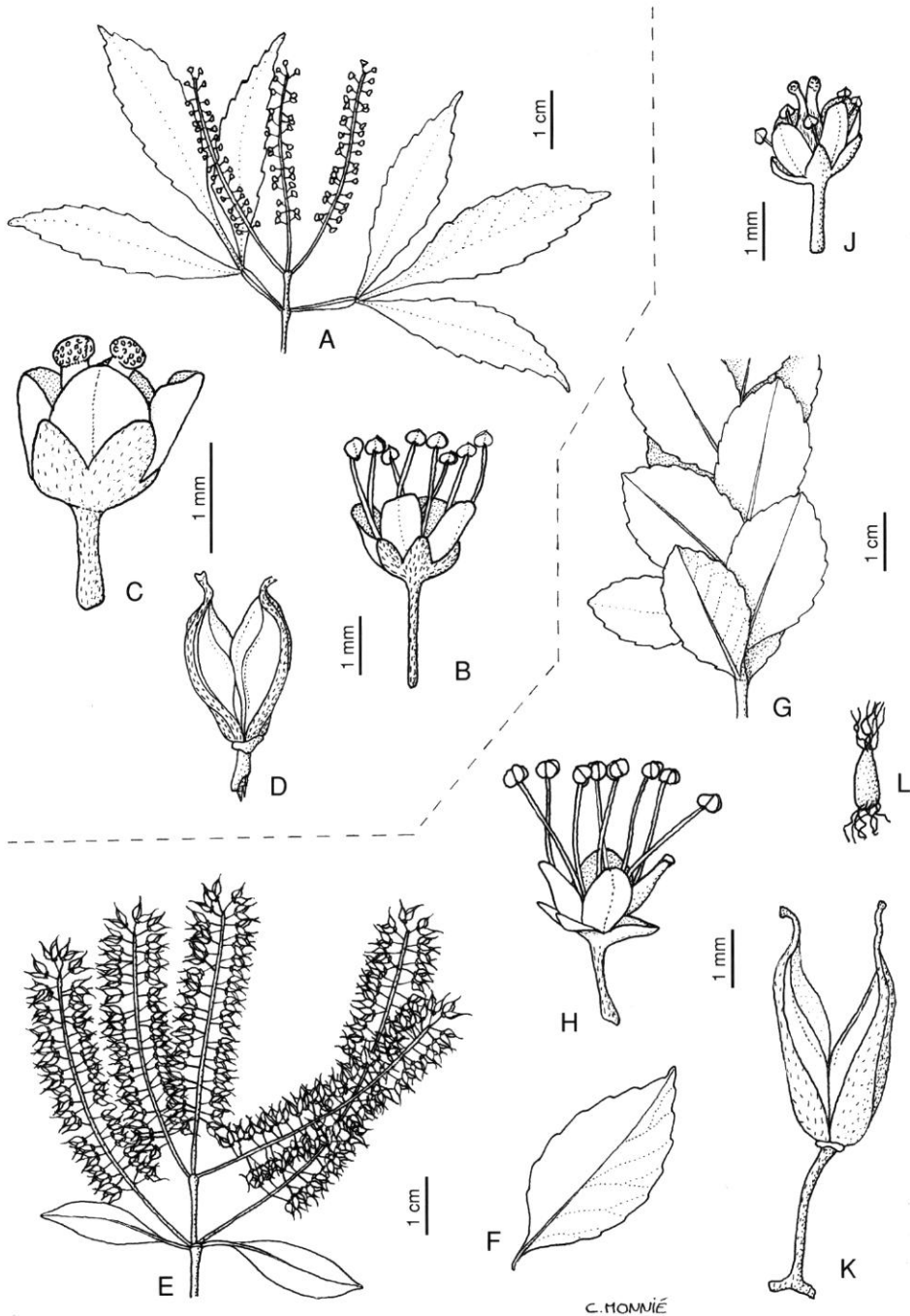


Fig. 3.—A-D, *Weinmannia raiateensis*: A, flowering stem, the inflorescence a triad, the stipules caducous; B, male flower; C, female flower; D, dehiscent capsule. (A, *Florence* 5143; B, *Gagné* 1457b; C, *Florence* 8945; D, *Florence* 3746).—E-L, *Weinmannia vescoi*: E, shoot with infructescence (pentad); F, single leaf; G, section of a stem with short internodes and imbricate leaves; H, male flower; J, female flower; K, dehiscent capsule; L, seed. (E, F, K, L, *Gagné* 1454; G, *Florence* 3586; H, *Florence* 5197; J, *Florence* 8991).—Drawn by C. MONNIÉ.

flower: filaments 0.8-1 mm long, disc lobes 0.7 mm long, ovary 1-1.2 mm long, \pm glabrous, styles 0.9-1 mm long, the stigmas capitate.

Capsules 1.5-3.2 \times 0.9-1.8 mm at dehiscence, the styles ca. 0.5 mm long, exocarp glabrous; calyx lobes caducous, central column present. Seeds 0.6 mm long, comose at both ends, the hairs short, 0.4 mm, and not very abundant.—Fig. 2, 3A-D.

JUVENILE FOLIAGE.—*Florence 3746b* consists of regrowth shoots from the base of the trunk. The leaves are 3-5-foliolate, chartaceous, and the apical leaflet is almost rhombic and broader than in the adult foliage.

BREEDING SYSTEM.—Limited herbarium material has only unisexual flowers, but this species is in fact polygamodioecious (J.C. BRADFORD pers. comm.).

FIELD CHARACTERS.—Leaves pale green. Inflorescence rachis purplish; buds white or cream; flowers pale yellow to white. Fruits red or pale purple.

DISTRIBUTION AND ECOLOGY.—Endemic to Raiatea where it is relatively widespread but rather scarce, from 300-965 m. A species typical of hygrophilous vegetation at mid altitude with *Metrosideros*, *Glochidion* and *Myrsine*, or in cloud forest with *Ilex*, *Macaranga* and *Astronidium*. It does not occur in the same habitats as *Weinmannia vescoi* (see below).

MATERIAL EXAMINED.—**SOCIETY ISLANDS: Raiatea:** *Florence 3554*, Plateau de Temehani Rahi, 16°47'S-151°27'W, 690 m, fr., 3 July 1982 (PAP); *Florence 3746*, *ibid.*, 760 m, fr., 25 Aug. 1982 (BISH, K, P, PAP); *Florence 3746b*, *ibid.*, regrowth, 25 Aug. 1982 (P, PAP); *Florence 3754*, *ibid.*, flanc NW, 740 m, fl., 25 Aug. 1982 (P, PAP); *Florence 5143*, côte E, Avera, Crête S de la Paipai, 16°48'S-151°26'W, 395 m, 13 Sep. 1983 (P, PAP); *Florence 8945*, Tevaitoa, crête sommitale du Mt. Toomaru, 16°50'S-151°27'W, 965 m, fl., 27 Nov. 1987 (P, PAP); *Gagné 1457b*, Mt. Temehani, NE side, 740 m, 3 Sep. 1977 (BISH, P).

BERNARDI (1964) placed *Weinmannia raiateensis* in synonymy under *W. vitiensis* Seem. on the basis of the type description. Both have trifoliolate leaves but in *W. raiateensis* they are generally smaller and more delicate, although there is some overlap. Several other species in sect.

Leiospermum in the Pacific have trifoliolate or imparipinnate leaves with a somewhat winged petiole, including *W. croftii*, *W. sp.* (Solomons A) and *W. denhamii* (HOPKINS 1998c). Although distinctions between taxa are slight, there are differences in mean leaflet shape and dimensions. This particular leaf morphology has thus either evolved several times or else these species originate from a single trifoliolate/imparipinnate ancestor that has been dispersed amongst a number of volcanic islands and differentiated only slightly on each.

3. *Weinmannia vescoi* Drake

Ill. Fl. Ins. Pacif.: 35, t. 13 (1886); Fl. Polynésie Franç.: 61 (1893); Bernardi, Bot. Jahrb. Syst. 83: 206 (1964).—Type: *Vescoi s.n.*, Tahiti (*sic*, but probably from Raiatea) (holo-, P!).

Weinmannia ovalifolia J.W. Moore, Bish. Mus. Bull. 102: 28 (1933).—Type: *Moore 95*, Society Islands, Raiatea, S facing slope along path to Mt. Temehani, 18 Sep. 1926 (holo-, BISH; iso-, BISH!, L!).

Low shrub to small, multi-stemmed tree 0.15-4 m high \times 5+ cm diameter. Stems often sparsely branched or unbranched for long sections; branching rarely dichotomous. Nodes thickened and "kneed", the internodes laterally contracted, 0.5-2.5(-7.5) long \times ca. 1 mm thick. Stems glabrous, smooth with fine longitudinal striations, lenticels few, on lower parts of stems. Whole plant largely glabrous except for sparse puberulence sometimes present on stipules, inflorescence axes, pedicels; leaves, calyx and exocarp often warty. Stipules usually caducous, elliptical, ligulate or rarely orbicular, 0.3-0.7 \times 0.2-0.4 cm, apex acute or rarely rounded, \pm flat or rarely recurved, \pm glabrous to puberulent. Leaves unifoliolate, (rarely trifoliolate and then the petiole winged), the petiole 0.2-0.6 cm long, the blade elliptical, broadly elliptical or ovate, 1.8-4.7(-6.4) \times 1-2.5(-5.5) cm, base truncate to acute and shortly decurrent, apex acute, obtuse or rounded, subcoriaceous to coriaceous, rarely punctate below, margin sometimes thickened, crenate, crenations more pronounced in smaller ovate or elliptical leaves, 9-12 notches on each side of each leaf, midrib raised and ridged above, prominent

below, secondary venation obscure, flat or slightly indented above, slightly raised below.

Inflorescence usually a pentad sometimes with two lateral triads, rarely a heptad, reduced leaves sometimes present at nodes within inflorescence; peduncles and rachis segments glabrous or sparsely puberulent, 0.5-1.2(-2.5) cm long, racemes 2.5-5 cm long. Floral buds inserted singly; floral bracts 0.7-1.4 mm long, \pm equal in length to buds or longer, ligulate to subcymbiform, minutely ciliate on margin, caducous. Flowers mostly unisexual, rarely bisexual; pedicel 1.4-2.1 mm; calyx lobes 0.6-1 mm long; corolla 1-1.7 \times 0.6-1.2 mm, oblong; disc lobes 0.3-0.6 mm; in male flowers: filaments 2.7-3.4 mm long, anthers 0.3-0.4 mm diameter, ovary 0.6-1.1 mm, styles 0.1-0.3 mm; in female flowers: filaments 0.7-1.2 mm long, ovary 1-1.5 mm, styles 0.7-1 mm, stigmas capitate, papillose; in bisexual flowers: filaments 1.5-3.3 mm, ovary 1.2 mm, styles 0.7 mm.

Capsules 2.1-4.0 \times 1.5-1.8 at dehiscence, styles 0.5-1 mm long, stigmas capitate, exocarp glabrous with longitudinal striations, endocarp sometimes separating from exocarp; calyx lobes caducous, central column present. Seeds ca. 0.8 mm long, comose at both ends, the hairs 0.3 mm long.—Fig. 2, 3E-L.

BREEDING SYSTEM.—Polygamodioecious. Most specimens have male or female flowers (e.g. *Moore 793*, *St. John 172555*, *Florence 5197*, male; *Florence 5203*, *8991* and *Hoogland 12929*, female), *Gagné 1454* has some apparently bisexual flowers, and *Grant 5197* has mature capsules and male flowers on the same shoot.

FIELD CHARACTERS.—Growth form rarely with a central trunk, but usually with numerous tall stems arising from the base; often distinctive with long, sparsely branched, stiff twigs with short internodes and thickened nodes, the twigs often well covered with unifoliate, opposite and decussate, elliptical to rounded leaves. *Morat 6996* shows an extreme growth form from dense scrub in an exposed, wind swept region of the plateau; it is a much branched chamaephyte, 15-20 cm high with small, rounded leaves. In such individuals the slender stems arise from a large woody root-mass, often visible at ground level (J.C. BRADFORD pers. comm.). Inflorescences

often short, congested, not projecting beyond the leaves. Rachis of inflorescence and calyx either green or purple-red; flowers similar to those of *W. parviflora* in colour and scent (J.C. BRADFORD pers. comm.).

DISTRIBUTION AND ECOLOGY.—Endemic to Raiatea where it is locally abundant from 355-740 m. One of the species confined to the plateaux of Temehani Rahi and Temehani Ute Ute where another endemic and symbol of the island, *Apetabia raiateensis* (Campanulaceae), also occurs. Locally co-dominant with *Metrosideros*, *Astronidium* and *Alstonia*, the herb layer dominated by Cyperaceae such as *Gabnia schoenoides* or *Machaerina bidwillii*.

SELECTED COLLECTIONS (from a total of 26 studied).—**SOCIETY ISLANDS: Raiatea:** *Florence 3586*, Plateau de Temehani Rahi, fin de la route, 16°46'S-151°27'W, 490 m, fr., 5 July 1982 (BISH, P, PAP); *Florence 5197*, Plateau de Temehani Rahi, secteur NE, 16°46'S-151°26'W, 510 m, fl., 16 Sep. 1983 (BISH, P, PAP); *Florence 8991*, Tevaitoa, sentier du Plateau Temehani Ute Ute, 16°47'S-151°28'W, 435 m, fl., fr., 29 Nov. 1987 (BISH, P, PAP); *Florence 10454*, Tevaitoa, Plateau de Temehani Rahi, 16°46'S-151°27'W, 530 m, fr., 10 June 1990 (BISH, PAP); *Gagné 1457* (P), *1457a* (BISH), Mt. Temehani, NE side, 740 m, buds, 3 Sep. 1977 (P, BISH); *Grant 5234*, Distr. Avera, Temehani, 1690 ft., fl., 29 Jan. 1931 (BISH); *Hoogland & Florence 12929*, N slopes of Plateau de Temehani rahi, 410 m, fr., 21 Mar. 1994 (MO, P, PAP); *Moore 793*, path to Mt. Temehani, S facing slope, fl., 1 Jan. 1927 (BISH); *Morat 6993*, montée au Temehani ute, 550 m, buds, 26 Aug. 1982 (BISH, K, P, PAP); *St. John 17255*, Temehani Plateau, 500 m, fl., fr., 5 Oct. 1934 (BISH, P); *Whistler 4906*, ibid., 650 m, fl., 3 Sep. 1981 (BISH).

The type, *Vescoi s.n.*, is labelled "Tahiti". The lower parts of the stems are glabrous although the most distal internodes are moderately hirsute and the stipules are ligulate. The inflorescence is not congested. The majority of collections from high altitude on Tahiti that have similar broadly ovate leaves (*Weinmannia parviflora*) have thicker, more densely pubescent stems, strongly recurved stipules and congested inflorescences. However, a few have glabrous stems and ligulate stipules and/or inflorescences which project beyond the foliage. The identity and provenance of *Vescoi s.n.* is thus problematical. It could either be regarded as an aberrant form of *W. parviflora*

from high altitude on Tahiti or treated, as here, as a mislabelled collection from Raiatea.

Weinmannia vescoi resembles *W. parviflora* from high altitude on Tahiti in several respects, especially in the broadly ovate, often coriaceous leaves, the short internodes and thickened nodes. However, it differs in having glabrous stems and stipules that are usually caducous, \pm flat and ligulate.

Although following the same synonymy as BERNARDI, our circumscription of this species differs considerably from his, and *St. John 17255* from Raiatea is the only one of the specimens cited by BERNARDI that is referred here to *Weinmannia vescoi*; all the others cited by him are from Tahiti and placed by us in *W. parviflora*.

4. *Weinmannia marquesana* F. Br.

Bernice P. Bishop. Mus. Bull. 130: 99 (1935); Bernardi, Bot. Jahrb. Syst. 83: 193 (1964).

a) *Weinmannia marquesana* var. *marquesana*

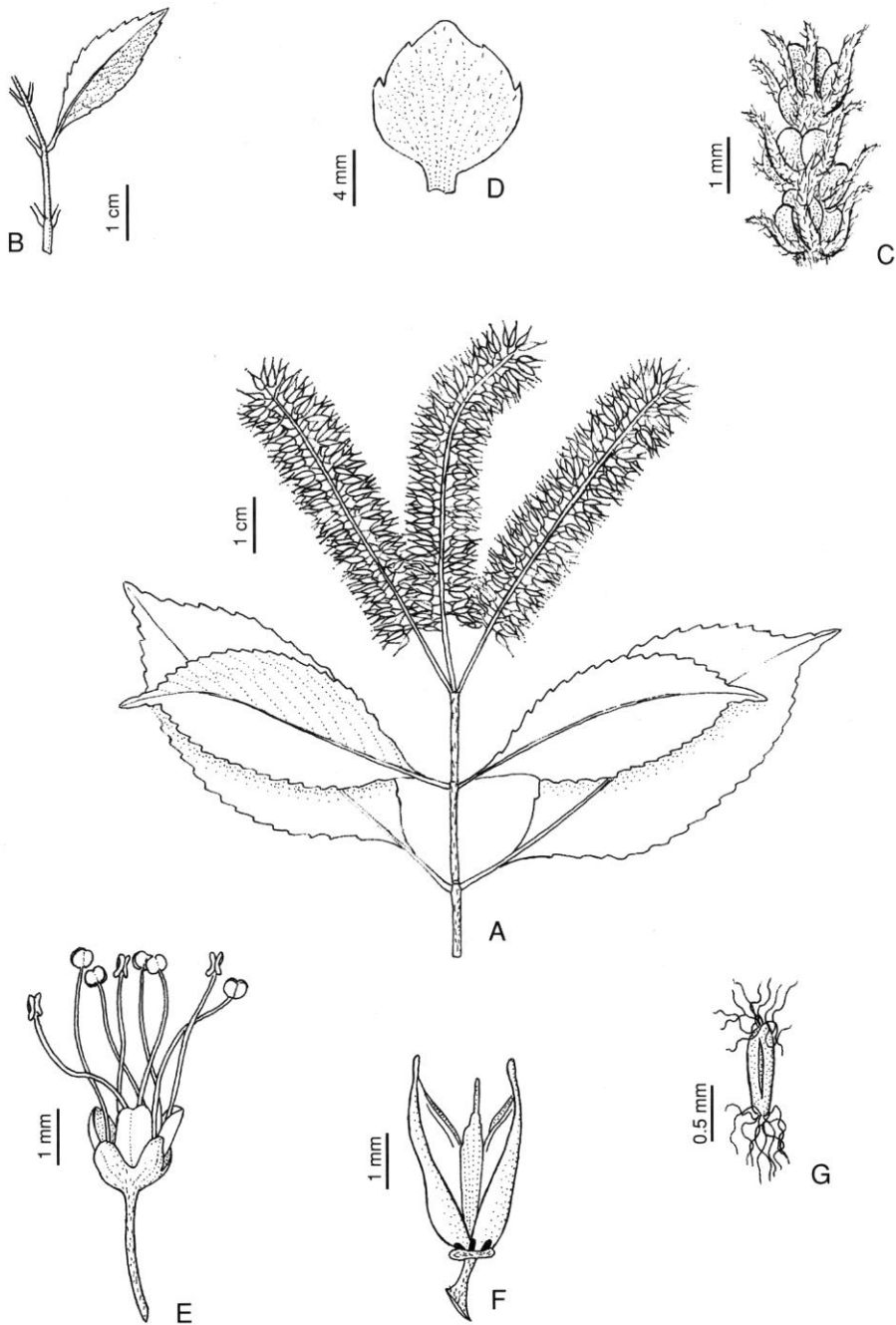
Weinmannia parviflora G. Forst. var. *marquesana* (F. Br.) Fosberg in Fosberg & Sachet, Micronesica 8: 44 (1972).—*Weinmannia marquesana* var. *typica* F. Br., Bernice P. Bishop. Mus. Bull. 130: 99 (1935), nom. inval.—Type: *Brown 497*, Marquesas Islands, Nuku Hiva, To(o)vii, 1000 m, 15 July 1921 (holo-, BISH; iso-, BISH!).

Weinmannia marquesana F. Br. var. *glabrata* F. Br., Bernice P. Bishop. Mus. Bull. 130: 99 (1935).—*Weinmannia parviflora* G. Forst. var. *glabrata* (F. Br.) Fosberg in Fosberg & Sachet, Micronesica 8: 45 (1972).—Type: *Brown 1084B*, Marquesas Islands, Hiva Oa, Mount Ootua, 800 m, 15 Dec. 1921 (holo-, BISH; iso-, BISH!).

Shrub to small tree, rarely a subshrub, (0.7-) 1.5-10 m tall, up to 35 cm dbh. Young stems terete and narrow, 1-2 mm diameter, the nodes slightly thickened, \pm glabrous to densely tomentose (the hairs up to 0.5 mm long) or pilose (hairs up to 0.9 mm long), older stems glabrescent, finely longitudinally fissured sometimes with pale lenticels. Branching often dichotomous. Stipules usually early caducous, either elliptical-ligulate, 0.6 \times 0.2 mm the apex rounded and recurved, or diamond-shaped to broadly ovate and conduplicate 1.3-1.7 \times 0.8-1.2 mm, the

apex acute and the margin entire to serrulate, glabrous except for short strigose hairs on abaxial surface towards the base. Leaves simple (rarely trifoliolate), petiole semiterete, 0.3-1.8 cm long, glabrous to tomentose along mid line on adaxial surface and glabrous or more often pubescent on abaxial surface, blade elliptical or sometimes ovate, (2.5-)3.3-7.5(-9.6) \times (1-)1.3-3.6(-4.4) cm, base cuneate or acutely constricted into the petiole, apex acute or sometimes acuminate, blade subcoriaceous, glabrous, sometimes punctate below, margin usually minutely thickened and revolute, minutely crenulate, crenate, serrate or rarely \pm sinuate, 11-22 notches down each side; main vein flat or raised above, and sometimes minutely hairy towards the base, prominent and often shortly hairy below, secondary and tertiary venation flat on both sides, the secondary veins equidistant from one another and all arcuate towards the margin and apex at the same angle, reticulum of tertiary veins open to dense.

Inflorescence a triad or pentad (variants include 3 triads or a central triad and 2 pairs of racemes (each developing from a lateral auxiliary bud) arising from the same node as the subtending leaves), reduced leaves at nodes within inflorescence not seen, peduncles and rachis segments 0.8-2.5(-6.5) cm long, almost glabrous or sparsely to densely hairy, racemes up to 7-8(-12) cm long. Floral buds inserted singly; floral bracts to 1.6 mm long, narrowly ligulate to subcarinate, strigose-puberulent, caducous. Flowers unisexual or bisexual; pedicel 1-3.0 mm long, puberulent or not; calyx lobes 0.7-1.2 \times 0.6-1 mm long, shortly strigose or glabrous on outer surface; petals oblong, 1.5-1.9 \times 0.8-1.2 mm, apex rounded; disc lobes 0.4-0.8 mm long; in male flowers: filaments 2.7-3 mm long, the ovary 0.8-0.9 mm long, usually pubescent, the styles ca. 0.2 mm long, curved inwards; in female flowers: filaments 0.4-0.5 mm long, the ovary 1.1-1.5 mm long at anthesis, glabrous, and the styles 1 mm long, \pm erect, the stigmas capitate and papillose, ovules up to 4 \times 7 per capsule; in bisexual flowers: filaments 2.8-3.5 mm long, ovary 1.5-2.2 mm long, glabrous or with sparse short strigose hairs, styles 1.2-1.4 mm long, stigmas capitate, papillose. Infructescence often dense.



C. MONNIÉ

Fig. 4.—A-G, *Weinmannia marquesana*: A, *W. marquesana* var. *marquesana*: shoot with infructescence of 3 racemes (triad), stipules caducous; B, *W. marquesana* var. *myrsinites*: leaf with dense reticulate venation; C, section of a raceme showing floral bracts and buds; D, stipule from a sterile shoot; E, male flower; F, fruit with persistent central column; G, seed. (A, Gagné 1033; B, MacKee 44689; C, Mercier s.n. 1847; D, Mumford & Adamson 494; E, Florence 7447; F, G, Florence 6882).—Drawn by C. MONNIÉ.

Capsules 3.3-5 × 1.5-2 mm at dehiscence, styles 0.5-1 mm long, exocarp glabrous or almost so, endocarp sometimes separating from exocarp in old fruits; calyx lobes caducous, central column present. Seeds 0.6-0.8 mm long, comose at each end, the hairs few and weakly developed, < 0.5 mm long.—Fig. 4A,C-G, 5.

JUVENILE FOLIAGE.—Foliage from young plants and coppice shoots is either simple (*Mumford & Adamson 139* and *Brown 1078*) or trifoliolate (*Mumford & Adamson 494*) with the stipules often persistent. As in other species, the leaflets are chartaceous or subcoriaceous. *Perlman 10204* from low forest on Hiva Oa is exceptional as it is almost glabrous, has trifoliolate leaves up to 23 cm long (terminal leaflets up to 17 × 8.5 cm) and the stipules are orbicular-reniform, 3.5 cm diameter, with the apex broadly rounded and the margin entire or dentate. This specimen is probably from a coppice shoot in shade.

BREEDING SYSTEM.—Polygamodioecious. Several sheets have male flowers and mature fruits and only 3 out of about 70 have female flowers (*Mumford & Adamson 497*, *Quayle 1253* and *Florence 7262*). There is no evidence of proandry. *Florence 7447* (P) has bisexual flowers and dehisced fruits and another sheet (BISH) has both male and bisexual flowers. This species appears to have cycles of male and bisexual flowers, with occasional plants producing female flowers.

FIELD CHARACTERS.—Variable in growth habit; when a small tree, the crown sometimes umbrella-shaped. Bark grey, brown or reddish, smooth; sapwood white or pinkish; heartwood red, fragrant. Flowers greenish-white to cream, calyx greenish-red, corolla and stamens white. Young fruits green to bright carmine red.

DISTRIBUTION AND ECOLOGY.—Marquesas Islands: Fatu Hiva, Hiva Oa, Nuku Hiva, Tahuata, Ua Huka, and Ua Pou, from 500-600 m upwards, except on Nuku Hiva where found from 790-1180 m.

This appears to be a sister species of *Weinmannia parviflora* from the Society Islands occupying the same range of habitats, from dense primary rain forest and disturbed forest at mid-elevations to cloud forest and scrub on ridges

and slopes, often in exposed localities, at high altitude. It also occurs in xerophilous scrub or open areas on hilltops with *Dicranopteris*, where it resprouts after burning. It is one of the major woody plants from 790 m upwards on Nuku Hiva, locally co-dominant and increasingly common with altitude. In dry forest, scrub and savanna its main associates are *Metrosideros* and *Dicranopteris*, and also *Paesia*. In mesic forest it occurs with *Cyathea*, *Freycinetia*, *Cheirodendron*, *Santalum*, *Scaevola*, *Myrsine*, *Ilex*, *Glochidion*, *Cyrtandra*, *Trimenia*, *Hernandia*, *Metrosideros*, *Mangifera*, *Pandanus*, *Hibiscus*, *Wikstroemia*, with numerous ferns and epiphytes.

SELECTED COLLECTIONS (from a total of 67 studied).—MARQUESAS: **Fatu Hiva:** *Brown 1078*, Omoa, 800 m, st., 4 Apr. 1905 (BISH); *Decker 2388*, along trail between Omoa and Ui'a, within 1 km of pass over central ridge, 750 m, fr., 12 Oct. 1974 (BISH, P); *Florence et al. 9490*, haut bassin de l'Uiha, E du Mt. Teamotua, 10°28'S-138°38'W, 660 m, fl., 21 July 1988 (BISH, P, PAP); *Gagné 1220*, Teauapuhiau Pass, above Ouia valley, 720 m, buds, 1-3 Aug. 1977 (BISH); *Wagner et al. 6152*, Ridge E of Mt. Teamotua from ridge below road along ridge to cascade, 640 m, fl., 21 July 1988 (BISH). **Hiva Oa:** *Brown 1084A*, Feani, 900 m, st., 5 Apr. 1905 (BISH); *Cherrier in MacKee 44711*, Mokoau, 500 m, fr., 13 Nov. 1989 (P, PAP); *Decker 1189*, Puamau, along Puamau-Atuona trail, 500-650 m, fl., 14 Dec. 1963 (L, P, PAP); *Kondo s.n.*, Mt. Tapeata, 2500 ft., fr., 15 Oct. 1969 (BISH); *Mumford & Adamson 414*, Mt. Ootua, W slope, 700 m, buds, fr., 25 May 1929 (BISH); *Mumford & Adamson 497*, NW summit of Mt. Temetiu, 3400 ft., fl., fr., 3 Aug. 1929 (BISH); *Oliver & Schäfer 3216*, Mt. Ootua, old trail E of summit, 640 m, fr., 26 Feb. 1975 (BISH, PAP); *Perlman 10204*, trail towards Hanamenu, 3200 ft., juv., 3 Aug. 1988 (BISH, PAP); *Perlman 10259*, Vaipahae Falls rd., 1700 ft., fr., 10 Aug. 1988 (BISH, K, P); *Sachet & Decker 1903*, road from Atuona to Puamau, just below Mt. Ootua, 625-700 m, fr., 23 Nov. 1974 (P, PAP). **Nuku Hiva:** *Florence 4303*, Toovii, épaulement au-dessus du réservoir, 8°52'S-140°09'W, 950 m, fr., 4 Dec. 1982 (BISH, P, PAP); *Florence 8421*, route Taiohae-Toovii, branche droite de la Ht. Taipivai, 8°53'S-140°08'W, 760 m, fl., 29 July 1987 (BISH, K, P, PAP); *Florence 4361*, route Toovii-Terre Déserte, km 6.8 après le col, 8°52'S-140°10'W, 960 m, fr., 9 Dec. 1982 (BISH, K, P, PAP); *Florence 8538*, Terre Déserte, crête Ouest du Mt. Akaupe, 8°52'S-140°10'W, 1180 m, buds, 10 Aug. 1987 (BISH, P, PAP); *Gagné 1033*, spur of Mt. Ooumu, Toovii plateau, 790 m, fr., 16 July 1977 (BISH, L, P); *Gillett 2215*, Toovii-Taiohae trail, 2 km from

Tapuaooa shelter, 800 m, fr., 4 Aug. 1970 (BISH, K, L, P); *Lorence et al.* 6089, Toovii region, NW of l'Économie Rurale complex along new rd. to airport, 1060 m, fr., 16 July 1988 (P, PAP). **Tabuata:** *Hallé* 2168, sommet, fl., fr., 17 Mar. 1973 (P); *Perlman et al.* 14911, summit of ridge above Vaitahu nr. Haaoiputeomo, nr. antenna, 2740 ft., fl., 1 Sep. 1995 (P); *Schäfer* 5499, Vaitahu, crête d'Amatea, 620 m, st., 10 Apr. 1975 (K). **Ua Huka:** *Florence* 7262, Hane, crête SW menant au Mt. Hitikau, 8°55'S-139°32'W, 540 m, fl., fr., 20 Feb. 1986 (P, PAP); *Quayle* 1679, s.loc., fr., 9 Nov. 1922 (BISH); *Quayle* 1758 (BISH); *Quayle* 1829, fl. (BISH); *Quayle* 1830, fr. (BISH). **Ua Pou:** *Quayle* 1188, fr., 12 Sep. 1922 (BISH).

LOCAL NAMES.—Atakua, Ata.

DISTINCTION FROM WEINMANNIA PARVIFLORA.—*Weinmannia marquesana* and *W. parviflora* are clearly closely related. Although BERNARDI (1964) regarded *W. marquesana* as distinct, FOSBERG & SACHET (1972) reduced it to a variety of *W. parviflora* (Table 1). We are once more giving it specific status although there is some overlap in characters (Table 2).

VARIATION WITHIN WEINMANNIA MARQUESANA.—This is a polymorphic species, varying in the size and shape of the leaves and the quantity

and length of the indumentum, and thus it shows much the same range in variation as *Weinmannia parviflora*. Because of the range in amount and type of indumentum, we agree with BERNARDI (1964) that *W. marquesana* var. *glabrata* can not be maintained. However, one particularly distinctive variant originally named by FOSBERG & SACHET (1972) is maintained here, var. *myrsinites*. Because of the variability of this species, it is not surprising that there are some intermediates between the two named varieties (see below).

Florence 7262 is a specimen of *Weinmannia marquesana* var. *marquesana* from Ua Huka with female flowers, dehiscent capsules and mostly trifoliolate leaves. In *W. parviflora* on Tahiti, occasional plants also occur with some trifoliolate leaves, either on the lower, sterile branches (e.g. *Hoogland & Florence* 12911) or on flowering branches (e.g. *Hoogland & Florence* 12915).

Florence 6882 from 1166 m on Nuku Hiva has a mixture of long and short, relatively thick and densely hairy internodes, and broadly elliptical or ovate leaves. It is thus vegetatively similar to collections of *Weinmannia parviflora* from high altitude on Tahiti. *Perlman et al.* 14911 from Tahuata has exceptionally narrow leaflets.

TABLE 2.—Comparison of the characters of *Weinmannia parviflora* and *W. marquesana* var. *marquesana*

Character	<i>W. parviflora</i> (at low and mid elevation)	<i>W. marquesana</i> var. <i>marquesana</i>
Shape of leaf blade	narrowly elliptical	elliptical to ovate
length-breadth ratio excluding petiole	1: (0.27-)0.3-0.37(-0.47)	1: (0.36-)0.39-0.5(-0.58)
Stipules	persistent, recurved elliptical, spathulate or ± orbicular apex rounded, margin entire	caducous, often conduplicate broadly ovate apex acute, margin often toothed (sometimes narrowly ligulate with rounded apex and entire margin)
Capsules at dehiscence	2.5-3.5 mm long	3.3-5 mm long
Inflorescence	complex, racemes usually arising from 3 successive nodes, up to 11 racemes per inflorescence (pentad + 6)	simple, racemes arising usually at 1 node or sometimes 2, triad or pentad (rarely otherwise)
Indumentum on young stems	dense indumentum of erect hairs to 0.5 mm long	variable, dense to sparse

b. *Weinmannia marquesana* var. *myrsinites*
(Fosberg & Sachet) H.C. Hopkins & J. Florence,
comb. nov.

Weinmannia parviflora G. Forst. var. *myrsinites*
Fosberg & Sachet, *Micronesica* 8: 45 (1972).—
Type: *Sachet & Decker 1155*, Marquesas Islands,
Hiva Oa, Atuona-Feani trail, 1200-1300 m, 24-26
Sep. 1963 (holo-, US!; iso-, BISH!, K!, L, NY, P!).

Shrub 0.6-1.5 m high, less commonly a small
tree 2 m. Internodes usually short, ca. 0.5 cm
long, nodes thickened, young stems strigose to
puberulous. Leaves ovate or elliptical, the blade

1.6-2.7(-3.3) × 0.7-1.7 cm, plus a petiole 1-
6 mm long, base cuneate or truncate, apex acute,
blade coriaceous, the upper side drying dark pur-
plish-brown, lower side dark chestnut, margin
with 8-12 notches on either side, venation usual-
ly obscure and flat above, secondary and tertiary
venation flat below and drying conspicuously
darker than intervenium, bases of secondary
veins frequently closer together in proximal part
of blade, and basal veins more strongly arched
towards apex than are the more distal ones, venation ± brochidodromous, reticulum of tertiary
veins dense.—Fig. 4B, 5.

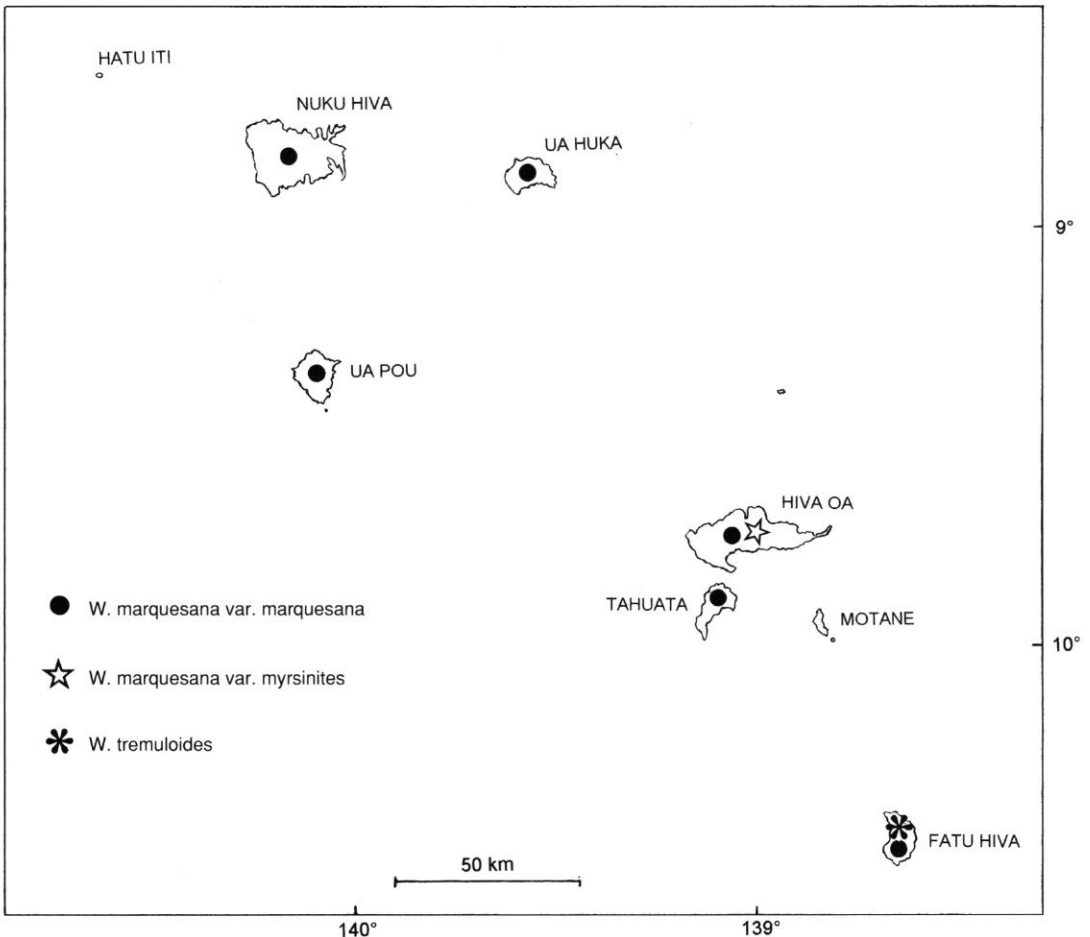


Fig. 5.—Distribution of *Weinmannia* in the Marquesas Islands.

FIELD CHARACTERS.—The inflorescences are much shorter than in *W. marquesana* var. *marquesana*. Flowers white; young fruits red.

DISTRIBUTION AND ECOLOGY.—Marquesas: Hiva Oa, 800-1300 m. Common in scrub on upper, exposed, windswept slope at crest of ridge (maquis sommital) on dry side of island and also on leeward side in cloud forest.

MATERIAL EXAMINED.—MARQUESAS: *Hiva Oa*: Brown 1098, Atuona, 800 m, st., Dec. 1921 (BISH); Cherrier in MacKee 44689, Feani, 1100 m, fl., fr., 11 Nov. 1989 (P, PAP); Florence & Perlman 9667, Atuona, piste de Hanameru, NW du Mt. Temetiu, 9°48'S-139°5'W, 1130 m, buds, fr., 30 July 1988 (BISH, K, P, PAP); Oliver & Schäfer 3138, Feani ridge, 1150 m, fr., 12 Feb. 1975 (BISH, PAP); Oliver & Schäfer 3148, *ibid.*, 1050 m, fr., 12 Feb. 1975 (BISH, P); Oliver & Schäfer 3155, *ibid.*, 1020 m, fr., 12 Feb. 1975 (BISH, P, PAP); Perlman 10198, trail towards Hanamenu, 3550 ft., buds, 3 Aug. 1988 (BISH, P, PAP).

TAXONOMY AND VARIATION.—This variant of *Weinmannia marquesana* has a very distinctive morphology, and since names are often useful for such entities, we retain it as an infraspecific taxon. However, since it occurs only in more exposed situations, it may perhaps be no more than an ecotype of *Weinmannia marquesana*. A few collections from Hiva Oa have leaves that are either intermediate between the two varieties or have characteristics of both on same twig (Oliver & Schäfer 3161, Perlman 10230, Sacht & Decker 1903, Decker 1189). Perlman 10130 (BISH, PAP) from Nuku Hiva has small leaves on stems with thickened internodes and dense erect hairs. Its venation is more similar to that of *W. marquesana* var. *marquesana* than var. *myrsinites* but the blades have dried almost black above and dark chestnut below. It is placed here with doubt.

5. *Weinmannia tremuloides* H.C. Hopkins & J. Florence, *sp. nov.*

Insignis inter omnes Gallicae Polynesiæ species lateraliter complanato petiolo; a W. raiateensi J.W. Moore *longiore petiolo, angustioribus stipulis, majoribus fructibus, majoribus seminibus munitis longioribus pilis, præcipue differt.*

TYPE.—Florence & Perlman 9581, Marquesas Islands, Fatu Hiva, W ridge of Mt. Mounanui, 10°28'S-138°37'W, 700 m, buds, fr., 26 July 1988 (holo-, BISH!; iso-, CHR!, P!, PAP!, PTBG!, US!).

Shrub ca. 2 m high. Branching sometimes dichotomous. Stems finely longitudinally fissured, internodes 0.8-3 cm long, nodes somewhat thickened. Plant almost entirely glabrous, except for buds which have strigose hairs ca. 0.5 mm long, and occasional strigose hairs on young stems, stipules and leaves. Stipules oblong to ligulate, 0.6-0.8 × 0.2 cm, caducous. Leaves trifoliolate, total length up to 9 cm including petiole 2.5-4.2 cm; petiole laterally compressed and U-shaped in cross-section; leaflets narrowly elliptical, the lateral ones 3.6-4.4 × 0.7-1 cm, sessile and unequal at base, apex acute; terminal ones 4.8-6 × 0.8-1.1 cm, base attenuate, apex acute; the blade subcoriaceous, not punctate below, the margin somewhat thickened, crenate, 13-16 notches on each side of a lateral leaflet; midrib raised above, prominent below, secondary and tertiary venation somewhat indented above and flat below.

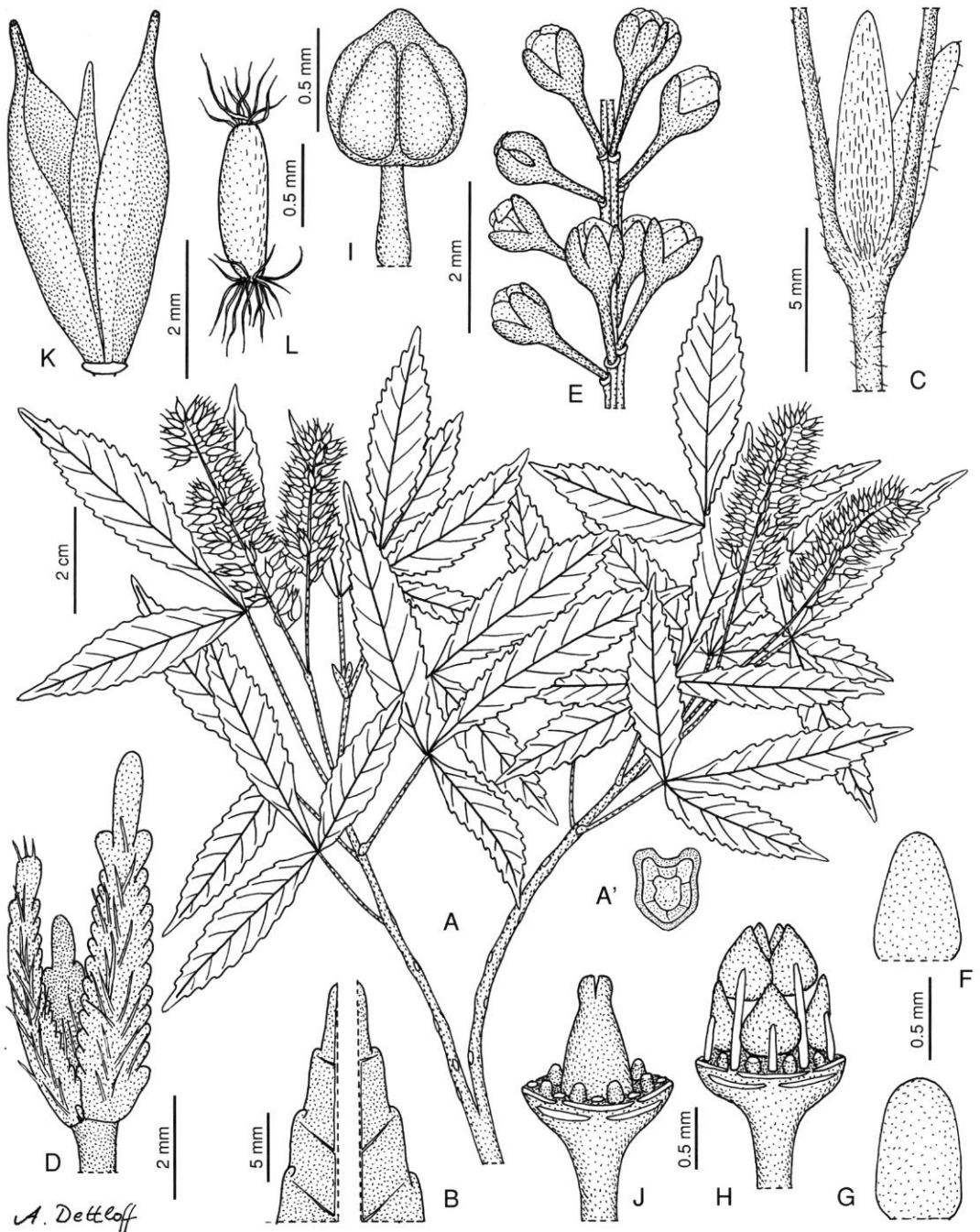
Inflorescence a central triad; peduncle and rachis segments glabrous; peduncle 1-1.7 cm long, rachis segments up to 6 cm long. Floral buds inserted singly; floral bracts ca. 1.1 mm long, ligulate, glabrous. Flowers at anthesis not seen. Calyx in bud glabrous.

Capsule 4-5 mm at dehiscence, the styles ca. 1 mm, exocarp sparsely hairy or ± glabrous; calyx lobes caducous, central column present. Seeds ca. 0.9 mm long, comose at both ends, the hairs 0.7 mm long.—Fig. 5, 6A-L.

FIELD CHARACTERS.—The foliage has a trembling appearance because of the long, laterally compressed petioles. Flower buds white. Dehisced capsules brown.

ECOLOGY AND DISTRIBUTION.—Known only from Fatu Hiva where it was found in low vegetation on ridge top and cliffs with *Metrosideros*, *Dicranopteris* and *Lycopodium*, and described as abundant from 700-850 m.

PARATYPE.—MARQUESAS: *Fatu Hiva*: Perlman & Florence 10175, slopes of Mounanui above Vaieenui Falls, 2300 ft., buds, 26 July 1988 (BISH).



A. Dettloff

Fig. 6.—A-L, *Weinmannia tremuloides*: A, fruiting shoot with trifoliolate leaves, the stipules caducous; A', cross section of grooved petiole; B, summit of leaflet, above (left) and below (right); C, stipules; D, summit of young shoot showing developing leaves; E, detail of inflorescence, the buds inserted singly; F, sepal, outside; G, petal, outside; H, immature flower with calyx and corolla removed to reveal androecium; I, immature anther; J, immature flower with calyx, corolla and androecium removed to reveal developing gynoecium; K, dehiscent fruit; L, seed. (A-L, Florence & Perlman 9581).—Drawn by A. DETTLOFF.

A well defined species. The leaflet shape is reminiscent of some specimens of *Weinmannia raiateensis* but the petiole is quite different. It is the most glabrous species in the region and the capsules are comparatively large, as in *W. marquesana*.

6. *Weinmannia rapensis* F. Br.

Bernice P. Bishop Mus. Bull. 130: 100 (1935); Bernardi, Bot. Jahrb. Syst. 83: 201, t. 35 (1964).—Type: *J. Stokes 306*, Rapa, Kulukulu [Kulukulu in protologue] or Onape, 140 ft., 13 Oct. 1921 (holo-, BISH; iso-, BISH!).

Shrubby tree 1.5-6 m high, up to 20 cm dbh. Branching usually dichotomous with central bud aborted or if developed, then less strongly so than lateral shoots. Young stems densely pubescent, older ones minutely longitudinally fissured, sometimes lenticellate. Buds in leaf axils often prominent. Stipules usually caducous, rarely seen, ca. 0.9 × 0.6 cm at node subtending inflorescence, ± glabrous on adaxial surface, strigose on abaxial one, apex obtuse, up to 1.1 × 0.9 cm on vegetative shoots, margin toothed. Leaves compound, leaflets usually 3 or sometimes 5; petiole semiterete, 1-2.5 cm long, rachis segments in imparipinnate leaves 1.5-3 cm, petiole and rachis densely pubescent on flattened adaxial surface; lateral leaflets elliptical to narrowly ovate, 2.8-6.9 × 1.1-2.8 cm, base unequal to dimidiate, apex acute; apical leaflets elliptical or obovate, 4.2-10.3 (including petiolule up to 2 cm) × 1.7-3.5 cm, somewhat larger than lateral leaflets, base often strongly attenuate to form a petiolule, apex acute to acuminate; leaflet blades glabrescent except for midrib which is densely pubescent above towards base and strigose below, coriaceous, rarely punctate below; margin thickened, sometimes undulate, markedly crenate, crenations 14-26 down each side and strongly acroscopic; midrib slightly raised above and prominent below, secondary veins flat or slightly raised above and below.

Inflorescence either a central pentad, the lower racemes subtended by fully developed leaves, reduced leaves or neither, or a pair of pentads or triads, each developed from an axillary bud and

the apical bud aborted. Inflorescence rachis segments 1-4 cm long, racemes up to 14 cm long. Auxiliary buds rarely seen, probably aborted. Stipules at nodes within inflorescence ovate, caducous, smaller than stipules at vegetative nodes. Floral buds inserted singly; floral bracts 1-2 mm long, caducous. Flowers male, female and bisexual; pedicel (1.3-)1.8-2.5 mm long, minutely hairy; calyx lobes shortly strigose or glabrous, sometimes warty, 0.9-1 mm long; petals oblong, 1.6-1.9 × 0.8-1 mm; filaments in male and bisexual flowers up to 2.5-3.5 mm long, in female flowers ca. 1.3-1.4 mm long, not always of equal length in any flower; disc lobes 0.5-0.7 mm long; ovary in male flowers 0.7-0.9 mm long plus styles 0.1 mm long, in female flowers 1.5-1.7 mm plus styles 1.2-1.5 mm long (at stage when anthers still present), variable in bisexual flowers according to age.

Capsules 2-3.5 mm at dehiscence, the styles 0.5-1 mm, exocarp glabrous with weak longitudinal ridges, sometimes warty, endocarp sometimes separating from the exocarp towards the apex; calyx lobes persistent or not, central column present. Seeds 0.7-0.8 mm long, comose at both ends.—Fig. 7A-E.

BREEDING SYSTEM.—Polygamodioecious. Different sheets of *St. John & Fosberg 15304* have male flowers and young fruits. *Hallé 7646* has morphologically male flowers in one inflorescence while another has bisexual ones. *A. Stokes 357* and *St. John & Maireau 15531* both have old female flowers.

FIELD CHARACTERS.—Bark rough, dark brown, sapwood reddish brown (*St. John 15305*). Leaves bright green, coriaceous. Inflorescence rachis red, flowers white; petals almost white, anthers flesh-coloured, calyx and young capsules red; both male and female flowers reported as having a faint fragrance like *Ceanothus* (*St. John*).

DISTRIBUTION.—Probably endemic to Rapa island.

POSSIBLE OCCURRENCE IN THE PITCAIRN GROUP.—BERNARDI (1964: 202) records this species from the Pitcairn Group citing *Cuming 1428* (K) from Elizabeth Island, now Henderson Island, and *Cuming s.n.* (G) from "Pitcairn (?)". There are two sheets at Kew labelled *Cuming*

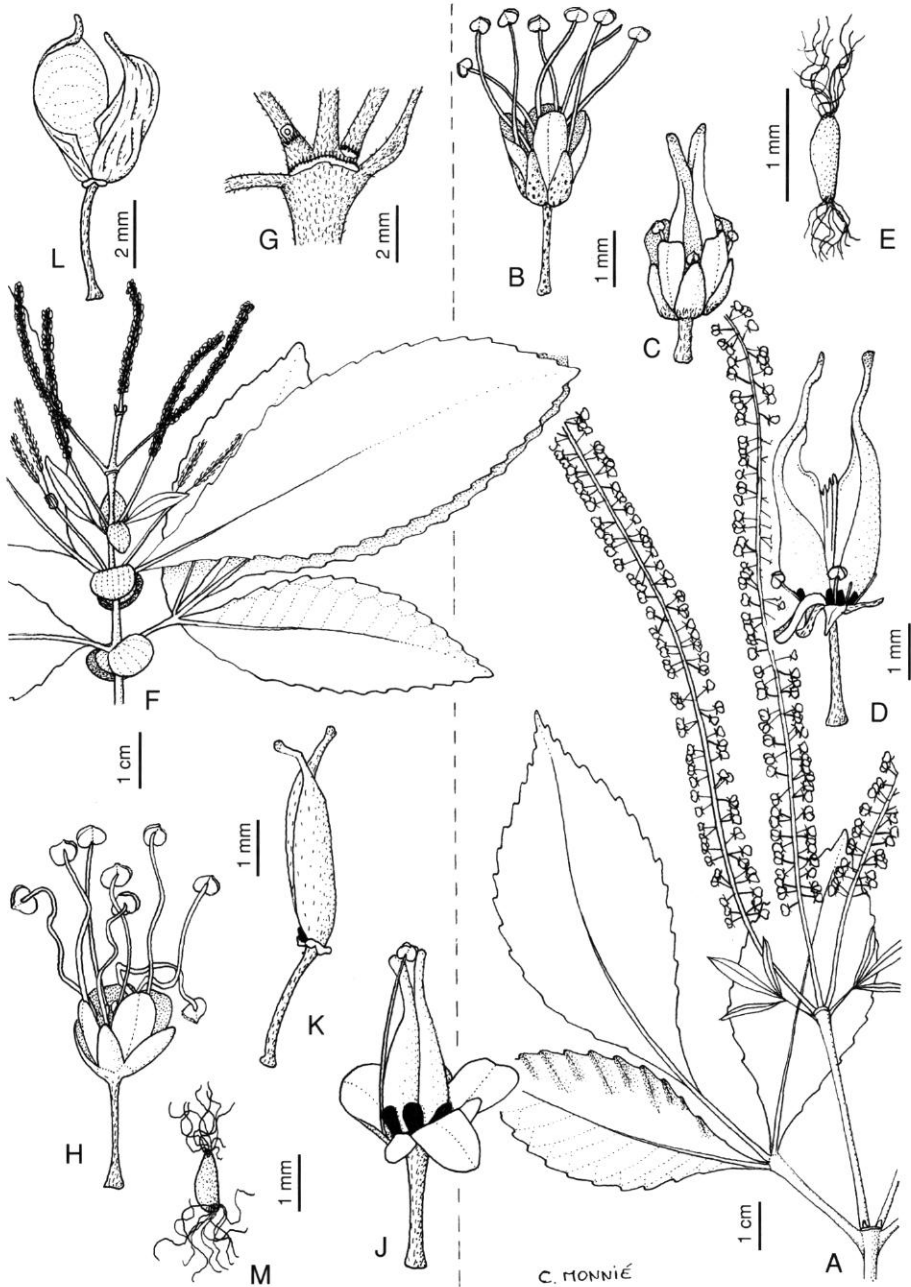


Fig. 7.—**A-E**, *Weinmannia rapensis*: **A**, shoot with trifoliolate leaves, the stipules caducous and inflorescence (1 of a pair of lateral triads with a pair of reduced leaves at node); note lateral auxiliary buds at bases of peduncles; **B**, male flower; **C**, female flower; **D**, capsule at dehiscence; **E**, seed. (A, Florence 6514; B, D, E, St. John & Fosberg 15304; C, Stokes 357.—**F-M**, *Weinmannia raro-tongensis*: **F**, shoot with simple and trifoliolate leaves, persistent stipules with revolute margin and immature inflorescence (pentad); additional inflorescences also developing in the axils of more proximal leaves; **G**, detail of node showing opposite petioles and the peduncles of 3 partial inflorescences; note scars close to the base of the two lateral peduncles and row of collaterals along stipular scar; **H**, male flower; **J**, female flower after anthesis, most of the stamens fallen; **K**, immature fruit; **L**, capsule at dehiscence; **M**, seed. (F, Merlin 306; G, K, Parks 22522; H, MacKee 44309; J, Gardner 2503; L, M, Wilder 543).—Drawn by C. MONNIÉ.

1428. One gives the locality "Elizth Island" and the other "Ins. Toubouia". The record from Elizabeth Island is doubtful for several reasons. Firstly, according to ST. JOHN (1940) *Cuming 1428* was collected on Toubouia, now Tubuai Island in the Austral Group. Secondly, recent extensive botanical collections on Henderson Island, including the area where CUMING collected, failed to find this species (FLORENCE et al. 1995; S. WALDREN pers. comm.). Thirdly it is known that some of CUMING's labels became mixed up resulting in erroneous records (S. WALDREN pers. comm.). If *Cuming 1428* is from Tubuai, it is the first record from an island other than Rapa; CUMING visited both Tubuai and Rapa (ST. JOHN 1940: 88). The date of collection on one sheet is given as 1831 but 1828 is considered correct (ST. JOHN 1940).

ECOLOGY.—From 30-220 m. Reported from forest on steep slopes and crest of ridge, where *Metrosideros* is dominant and also from *Dicranopteris-Metrosideros* scrub on exposed slopes. Other associates include *Myoporum*, *Corokia* and *Fitchia*. Sometimes very abundant and forming thickets (*Hallé 7646*) but generally less common than is *Weinmannia parviflora* on Tahiti. Rapa island is colder and wetter than the Society and Marquesas Islands, since it lies farther south and its climate is influenced by cool, damp air currents from Antarctica (see PASTUREL 1993).

MATERIAL EXAMINED.—**AUSTRAL ISLANDS: Rapa:** *Cuming 1428*, Rapa or Tubuai (K); *Florence 6395*, crête E vers Mt. Morongouta, 27°37'S-144°21'W, 210 m, fl., fr., 2 Feb. 1984 (BISH, K, P, PAP); *Florence 6514*, collines du NW de la baie de Haurei, 27°36'S-144°21'W, 50 m, fl., 6 Feb. 1984 (BISH, P, PAP); *Florence 6517*, S de Haurei, épaulement N du Mt. Maugaoa, 27°37'S-144°20'W, 75 m, fl., 7 Feb. 1984 (BISH, P, PAP); *Hallé 7501*, N vallée Hiri, 150 m, st., 2 Feb. 1984 (P); *Hallé 7517*, Morogo-Uta, 200-220 m, st., 2 Feb. 1984 (P); *Hallé 7646*, E du fond de la baie d'Ahurei, 30 m, fl., 6 Feb. 1984 (P); *Hallé 7700*, N de l'île Karapoo Rahi, fr., 9 Feb. 1984 (P); *Longfield 772*, s.loc., 11 Apr. 1925 (BM, K); *Paulay 29*, Maungaaiai, 250-350 m, 22 Jan. 1980 (A); *Raoul s.n.*, s.loc., fl. (P); *A. Stokes 2*, s.loc., 100 m, fl., 6 June 1921 (BISH); *A. Stokes 357*, Maungaaiae, 900 ft., fl., 19 Oct. 1921 (BISH); *St. John & Fosberg 15304*, Area, 75 m, fl., 1 July 1934 (A, BISH, L); *St.*

John & Fosberg 15305, *ibid.*, fl., fr., 1 July 1934 (A, BISH, K, L); *St. John & Maireau 15531*, Kaimaru, S ridge of Mt. Perahu, 400 m, fl., 13 July 1934 (BISH); *Varney 24*, piste de Hiri, 35 m, fl., 3 Jan. 1990 (P).

LOCAL NAME.—Aito. Local uses: fire wood and canoe parts (*A. Stokes 357*).

Rather uniform and distinctive. Most similar to *Weinmannia rarotongensis* (Fig. 7F-M), endemic to Rarotonga, the chief island of the Cook Islands, from which it differs by having uniformly trifoliolate leaves and being more velutinous on the stems and petioles. The branching is more often dichotomous and the crenation of the leaflet margins are more acroscopic. The stipules are usually caducous and not markedly recurved as in *W. rarotongensis*.

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INDEX TO TAXA AND SYNONYMS OF WEINMANNIA

This index includes all the taxa treated in the current revision of the Malesian-Pacific species (this paper and HOPKINS 1998a,b,c, all published in *Adansonia*, sér. 3, 20), thus some page numbers refer to the previous papers. Accepted names are in ordinary type, *synonyms* in italics, **new names** in bold, and invalid names in brackets. **F** = sect. *Fasciculata*, **L** = sect. *Leiospermum*.

- Arnoldia fraxinifolia* Blume = *Weinmannia fraxinea* (D. Don) Miq.
heterophylla Blume = *Weinmannia fraxinea* (D. Don) Miq.
pinnata Blume = *Weinmannia fraxinea* (D. Don) Miq.
 [*Cortex papetarius* Rumph.] = *Weinmannia fraxinea* (D. Don) Miq.
Leiospermum parviflorum (G. Forst.) D. Don = *Weinmannia parviflora* G. Forst.
Marattia terminalis Sol. = *Weinmannia parviflora* G. Forst.
 [*Merretia terminalis* Banks & Sol. mss] = *Weinmannia parviflora* G. Forst.
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borneensis Engl. = *Weinmannia fraxinea* (D. Don) Miq.
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var. marquesana (F. Br.) Fosberg in Fosberg & Sacht = *Weinmannia marquesana* F. Br. *var. marquesana*
marquesana
var. myrsinites Fosberg & Sacht = *Weinmannia marquesana* F. Br. *var. myrsinites* (Fosberg & Sacht)
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tannaensis Guillaumin = *Weinmannia denhamii* Seem.
thornei Guillaumin = *Weinmannia paitensis* Schltr.
tomentella Schltr. = *Weinmannia fraxinea* (D. Don) Miq.
tremuloides H.C. Hopkins & J. Florence **L**, p. 123
trichophora L.M. Perry = *Weinmannia urdanetensis* Elmer
urdanetensis Elmer **F**, p. 65, 74
versteeghii L.M. Perry = *Weinmannia pullei* Schltr.
vescoi Drake **L**, p. 116
virgulata Schltr. = *Weinmannia pullei* Schltr.
vitiensis Seem. **L**, p. 98
ysabelensis L.M. Perry **F**, p. 82
sp. (New Guinea A), p. 79
sp. (Solomons A) **L**, p. 84
sp. (Solomons B) **L**, p. 84
sp. (Sulawesi A) **F**, p. 55
Windmannia blumei (Planch.) Kuntze = *Weinmannia fraxinea* (D. Don) Miq.
fraxinea (D. Don) Kuntze = *Weinmannia fraxinea* (D. Don) Miq.
horsfieldii (Miq.) Kuntze = *Weinmannia fraxinea* (D. Don) Miq.
sundana (Miq.) Kuntze = *Weinmannia fraxinea* (D. Don) Miq.

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